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Co-introduction vs ecological fitting as pathways to the establishment of effective mutualisms during biological invasions

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Summary

Interactions between non-native plants and their mutualists are often disrupted upon introduction to new environments. Using legume–rhizobium mutualistic interactions as an example, we discuss two pathways that can influence symbiotic associations in such situations: co-introduction of coevolved rhizobia; and utilization of, and adaptation to, resident rhizobia, hereafter referred to as 'ecological fitting'. Co-introduction and ecological fitting have distinct implications for successful legume invasions and their impacts. Under ecological fitting, initial impacts may be less severe and will accrue over longer periods as novel symbiotic associations and/or adaptations may require fine-tuning over time. Co-introduction will have more profound impacts that will accrue more rapidly as a result of positive feedbacks between densities of non-native rhizobia and their coevolved host plants, in turn enhancing competition between native and non-native rhizobia. Co-introduction can further impact invasion outcomes by the exchange of genetic material between native and non-native rhizobia, potentially resulting in decreased fitness of native legumes. A better understanding of the roles of these two pathways in the invasion dynamics of non-native legumes is much needed, and we highlight some of the exciting research avenues it presents.

I. Introduction

Mutualistic interactions (e.g. pollination, seed dispersal, etc.) are essential for many plants to complete their life cycle and to increase their fitness. In communities, interacting species pairs are embedded within complex interaction networks (Fig. 1), where different nodes (e.g. plant taxa and their associated pollinator taxa) are connected by pairwise interactions (links). Mutualisms are often disrupted for non-native plants introduced into new areas with distinct mutualistic networks, often with negative consequences for their establishment success (Traveset & Richardson, 2014). These negative impacts can be circumvented if plants are co-introduced

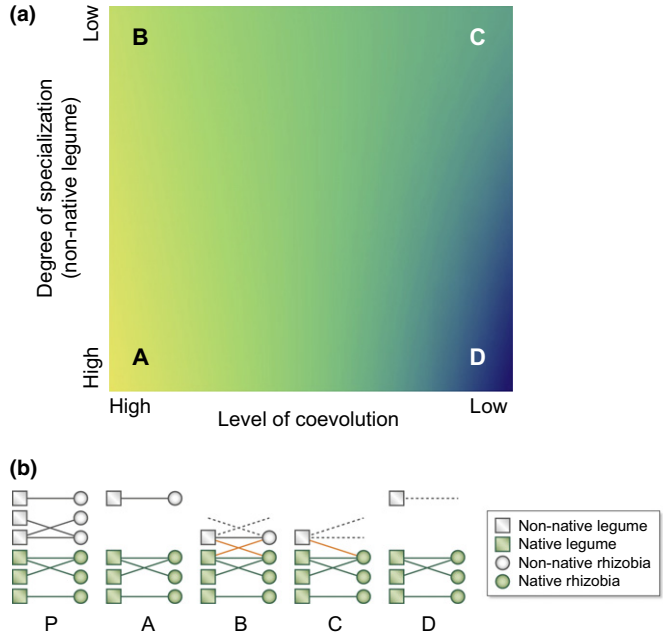


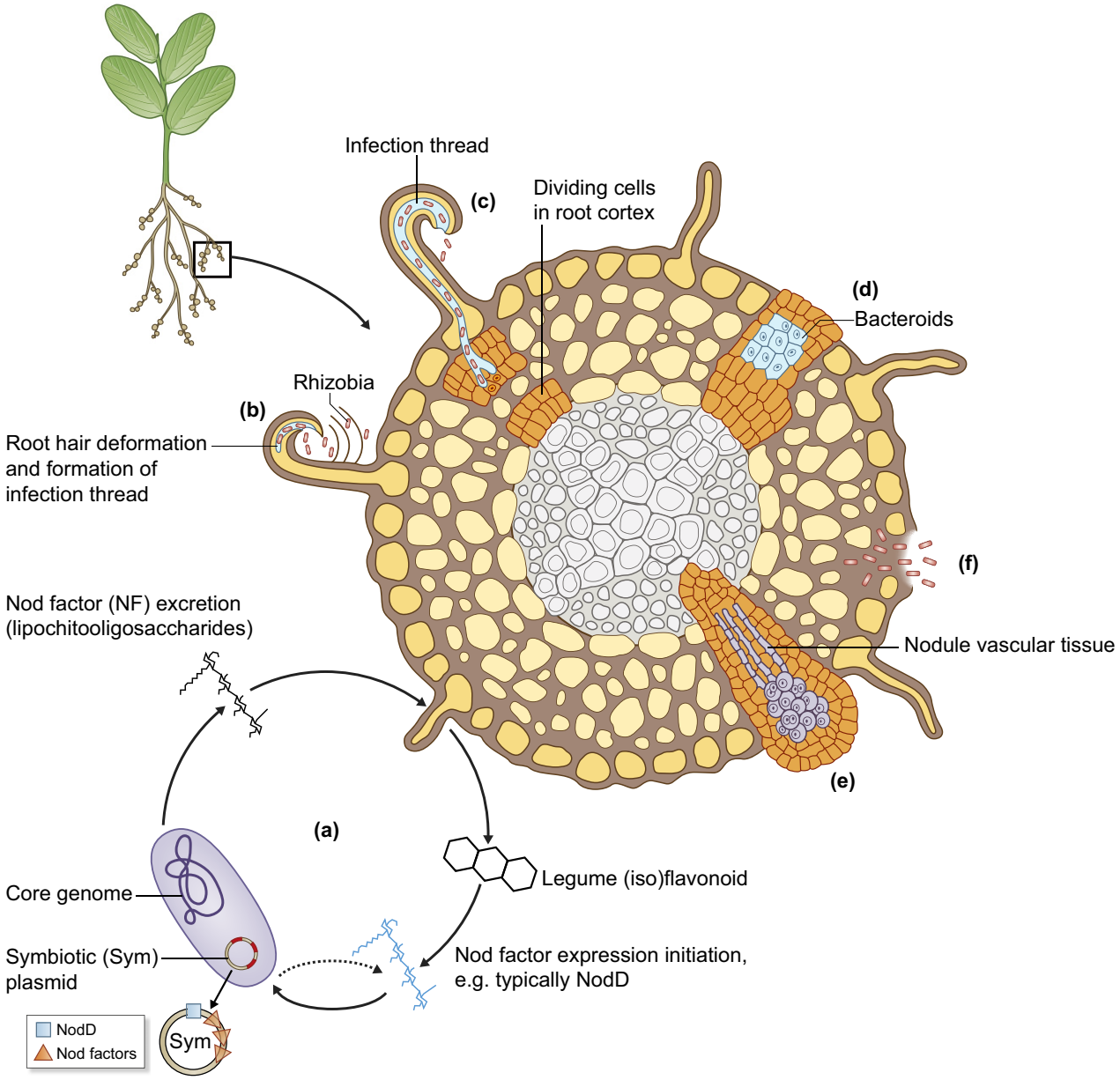
Fig. 1 Conceptual framework for inferring establishment success and invasion performance of introduced legumes from their symbiotic interaction with rhizobia. (a) The performance (yellow, high; blue, low) is visualized on the plane of coevolution (shared phylogenetic history between the invading legume and the rhizobia with which it interacts in the invasion range) and interaction specialization (ranging from interactions between specialist legumes and specialist rhizobia to those between generalist legumes and generalist rhizobia). Capital letters indicate four possible introduction scenarios. (b) Expected interaction network structures under each of these scenarios are indicated (A–D). Legumes are on the left of networks and rhizobia are on the right. P, pre-introduction networks (dashed lines, missing coevolved mutualisms; red lines, potential new associations). Scenario A: legumes co-introduced with specialized and coevolved rhizobia have a high level of performance. Co-introduced specialized species pairs form separate, unconnected motifs in the mutualistic network (network modularity). Thus, while they do not disrupt native interaction networks directly, they can rapidly alter soil nutrient cycling through ecosystem engineering, with native plants and soil rhizobia being replaced/excluded through altered abiotic conditions. Scenario B: legumes co-introduced with coevolved but promiscuous rhizobia lack specialized mutualists and have a moderately high level of performance. Introduced legumes can establish symbioses with resident generalist rhizobia, thus affecting resident native legumes interacting with the same generalist rhizobia. Introduced promiscuous rhizobia could jump hosts in the new environment and negatively affect resident native legumes. Scenario C: promiscuous legumes can establish symbioses with existing (native or non-native) soil rhizobia in the new environment and have a moderately low level of performance. Introduced legumes are likely to establish symbioses with promiscuous resident rhizobia. Scenario D: specialized legumes lacking coevolved rhizobia in the new environment have poor performance, which may lead to failed establishment.

with their coevolved mutualists, or are able to replace lost interactions with novel associations with resident mutualists (i.e. by infiltrating resident mutualistic networks; Hui & Richardson, 2017). By default, the strength of mutualistic interactions is molded through coevolution (Ehrlich & Raven, 1964), that is, strong reciprocal selection between interacting partners. However, coevolution is inadequate as an explanation for rapid formation of new biotic interactions in novel community contexts, such as those created by species invasions (Petanidou *et al.*, 2008). Janzen's (1985) proposal of ecological fitting may better explain such novel interactions between species that share little coevolutionary history. That is, species can switch their mutualistic partners in response to context-dependent changes, such as the temporal shift in the availability of old vs new mutualists that occurs during biological invasions (Valdovinos *et al.*, 2010). Certain key traits, such as interaction promiscuity, are likely to be important determinants of the probability of species fitting ecologically into novel community contexts, that is, being able to integrate into existing community interaction networks. Plant mutualisms range across the full spectrum of specialization, from highly promiscuous (generalist) to strongly specialized interactions (Bascompte, 2009). Plant establishment success and subsequent invasion performance should therefore be understood along axes representing both the amount of shared coevolutionary history and interaction specialization with mutualists (Fig. 1).

II. Specificity and effectiveness of legume–rhizobium interactions and their impacts on non-native legume establishment

Both the overrepresentation of legumes (family Fabaceae) in invasive floras (Daehler, 1998) and their often-severe impacts (e.g. Castro-Díez *et al.*, 2014) partly reflect their ability to form mutualistic interactions with nitrogen-fixing rhizobia. Rhizobia are a nonmonophyletic group of diverse bacteria within the Alpha- (alpha rhizobia) and Betaproteobacteria (beta rhizobia) classes. Rhizobia are capable of forming specialized structures (root, or less-frequently stem, nodules) on most legumes (Box 1). Rhizobia can fix atmospheric nitrogen within nodules that legumes can utilize, while simultaneously receiving carbon resources from the plant. Degrees of legume–rhizobium interaction specificity are modulated by intricate molecular mechanisms (Box 2), and can thus be shaped by gene-for-gene coevolutionary processes (Spaink, 2000). However, coevolution at the organismal level is complicated in rhizobia by the frequent horizontal gene transfer (HGT) of symbiotic gene clusters housed on highly mobile symbiotic plasmids or islands, sometimes even between different bacterial genera (Ding & Hynes, 2009). The potential therefore exists for rhizobia that share no evolutionary history with a potential host legume to circumvent the coevolutionary process by acquiring clusters of coevolved symbiotic genes horizontally (e.g. Horn *et al.*, 2014). As for most other mutualisms, legume–rhizobium interactions are theoretically susceptible to cheating strategies. However, available evidence suggests that the fitness of legume hosts and rhizobia is generally aligned, and there is no evidence to support the cheating hypothesis expectation of increased fitness of ineffective vs effective nitrogen-fixing bacteria (e.g. Checcucci *et al.*, 2016). This could reflect the existence of strong host control of the interaction through mechanisms like partner choice (Lira *et al.*, 2015) or sanctioning (Kiers *et al.*, 2003). However, partner choice is not perfect, as nodules often house ineffective bacteria, with recent evidence suggesting that, in some instances, nodules can be colonized by a range of non-N-fixing rhizobia or even nonrhizobial bacteria (Birnbaum *et al.*, 2016; Busby *et al.*, 2016; Checcucci

Box 1 Legume–rhizobium interactions



Successful symbiosis between legumes and rhizobia involves intricate molecular signal exchange. Generally, various rhizobial nodulation genes (*nod* genes) respond in a cascading fashion to plant root exudates, typically (iso)flavonoids. *Nod* genes encode for nodulation factors (NF) and are located on symbiotic (Sym) plasmids or mobile symbiotic islands that are transferable through horizontal gene transfer (HGT), even among distantly related rhizobia (Ding & Hynes, 2009). It is therefore common to find incongruences between phylogenies based on nuclear vs Sym plasmid genes. Root exudates of legumes activate rhizobial *nodD* regulatory proteins and, in turn, various nodulation genes, to produce NFs (lipochitooligosaccharides, a). NFs trigger several responses in legumes, such as ion fluxes and calcium spiking, leading to root hair deformation, rhizobial entrapment (b, c) and, ultimately, root nodule formation (d, e). Variations exist between different legume–rhizobium interactions in terms of excreted plant compounds, regulators besides *nodD*, and strain-specific combinations of nodulation genes (e.g. Lira *et al.*, 2015) and several interaction pathways between NFs and plant receptors have been identified (Spaink, 2000). On the other hand, a small number of rhizobial lineages are capable of NF-independent nodulation (Giraud *et al.*, 2007). Here, rhizobia can enter the host plant via cracks in the epidermis (f). Exact molecular mechanisms of such NF-independent interactions remain largely unknown, but evidence suggests that these bypass the early NF-dependent signaling pathways described earlier. Inside root nodules, rhizobia are capable of fixing atmospheric nitrogen primarily into NH_3 through nitrogenase activity.

Box 2 Legume–rhizobium specificity

Molecular signal exchange between legumes and rhizobia is a key component of symbiotic specificity (Lira *et al.*, 2015). Specificity in legume–rhizobium associations occurs at various taxonomic levels. For example, cultivars of one legume species that differ in specificity to a single rhizobium strain would be regarded as highly specific, as would a legume genus that only interacts with a single lineage of rhizobium. Such patterns indicate strong evolutionary specialization at the genotype level.

The excretion of exudates by legumes is an important determinant of symbiotic compatibility. For example, both the number and concentration of exudates seem to increase when compatible rhizobia are detected by host legumes (Lira *et al.*, 2015). Initial signal exchange by legume exudates may activate three main groups of nodulation genes in rhizobia: the common *nodABC* genes present in almost all rhizobia, encoding the basic structure of nodulation factors (NFs); host-specific *nod* genes (e.g. *nodEF*, *nodG*, etc.) whose expression can modify basic NFs, leading to host specificity; and regulatory genes (e.g. *nodD*) that are linked to the activation and transcription of both the common and specific nod genes. In turn, rhizobial NFs are recognized by so-called legume host Nod factor receptors (Lira *et al.*, 2015). Lastly, some rhizobia secrete additional proteins involved in nodulation, known as nodulation outer proteins (*Nops*). *Nops* may suppress the host plant's immune responses following infection, or they may modulate root cell cytoskeletal rearrangement during nodule development (Soto *et al.*, 2009).

et al., 2016). In general the determinants of both symbiotic effectiveness (i.e. N-fixation rates) and nodulation efficiency (i.e. bacterial competitiveness) are not well understood. The interaction between the host and bacterial genotype is consistently important (Lira *et al.*, 2015), that is, symbiotic efficiency is higher for some host–bacterium combinations than for others. Intuitively, higher efficiency might be expected for species pairs with shared coevolutionary history or stronger interaction specialization. While some studies support this relationship (e.g. Rodríguez-Echeverría *et al.*, 2012), the pattern is in fact difficult to gauge because studies seldom use potentially coevolved species pairs (i.e. host cultivars from which bacterial strains are isolated) when quantifying effectiveness and nodulation efficiency (Friesen, 2012). In addition, symbiotic efficiency of pairwise interactions can be strongly context-dependent (Heath & Tiffin, 2007), with outcomes influenced by an array of soil abiotic (e.g. pH, moisture, etc.) and biotic conditions (Vuong *et al.*, 2016). It is therefore clear that the probability of rhizobial co-introduction, along with degrees of symbiotic specialization, and symbiotic effectiveness are crucial elements affecting the establishment success and performance of introduced non-native legumes (Fig. 1).

III. Co-introduction and ecological fitting: two pathways to establish legume–rhizobium interactions during biological invasions

Intuitively, highest establishment success and subsequent invasion performance are expected when plants are co-introduced with specialized and coevolved rhizobia (Fig. 1a), followed by promiscuous plants co-introduced with coevolved but generalist rhizobia (Fig. 1b) or establishment of novel interactions with generalist resident rhizobia (Fig. 1c). Alien legumes might fail to establish when highly specialized plants, in the absence of co-introduced rhizobia, are unable to establish novel associations with resident rhizobia (Fig. 1d). These expectations satisfy several existing conceptual hypotheses to predict how soil microbial–plant mutualism specificity and co-introduction history influence plant invasion success (Birnbaum *et al.*, 2012). The importance of these scenarios for establishment success will be dependent on the extent to which legume–rhizobium interaction network assembly is determined by co-introduction (and thus possibly coevolution), vs ecological fitting (Fig. 1). If effective interactions are most likely between plants and bacteria sharing a coevolutionary history, we might expect successful invasions to conform most frequently to a co-introduction scenario (Fig. 1a), whereas an ecological fitting scenario (Fig. 1c) is likely if plants are flexible in their symbiont requirements and/or rhizobial lineages/functional types are widespread globally.

Recent work has detected substantial differences in nodule rhizobial communities in the native and non-native ranges of some legumes (e.g. Callaway *et al.*, 2011; Shelby *et al.*, 2016). In these instances, mutualism establishment in the non-native range probably did not involve co-introduction of rhizobia. On the other hand, it appears that co-introductions of legumes and rhizobia are more common than general wisdom would predict. That is, many legumes often harbor identical interacting rhizobia in both native and non-native ranges (e.g. Ndlovu *et al.*, 2013; Horn *et al.*, 2014; Birnbaum *et al.*, 2016; McGinn *et al.*, 2016). For example, rhizobial diversity associated with the globally invasive genus *Mimosa* (*M. pudica*, *M. pigra* and *M. diplotricha*) shows structured biogeographic patterns in both their native and invasive ranges. For these legumes, independent co-introductions with their native rhizobia have been illustrated in their non-native ranges in Australia (Parker *et al.*, 2007), China (Liu *et al.*, 2012) and Taiwan (Chen *et al.*, 2005). *Mimosa pudica* invasions in India illustrate the potential importance of such co-introductions where the species only nodulate with co-introduced beta rhizobia and appear unable to utilize alpha rhizobial strains that are associated with co-occurring endemic Indian *Mimosa* species (Gehlot *et al.*, 2013). In fact, alpha rhizobial nodules on *M. pudica* are ineffective or only partially effective (Melkonian *et al.*, 2014). In general, very little is known about how rhizobia are co-introduced with legumes, but their free-living nature in soils, or presence within root nodules, suggests transport of seedlings in soil as a likely mechanism. On the other hand, compatible rhizobia may be found in novel regions as a result of human-mediated dispersal, such as for crop inocula (Ambrosini *et al.*, 2016).

IV. Consequences of co-introduction of rhizobia and non-native legumes for invasion impacts

Importantly, invasion impacts – the nature of the impacts, the rate at which they accrue and their severity – might differ profoundly if the establishment of mutualisms during invasion occurs through

the co-introduction or ecological fitting pathways. The ecological fitting pathway involves negative influences on invasion performance through direct competition with native plants for available mutualists (i.e. a possible form of biotic resistance), whereby native legumes might be superior in attracting resident rhizobia. These negative effects may be amplified if novel associations between non-native legumes and native resident rhizobia have low symbiotic effectiveness (Fig. 2). While these effects will probably diminish during the course of invasion, as relative abundance of invasive plants and their recruited microbes increases and fine-tuning of the novel mutualism occurs, they may result in substantially longer lag times in invasions under ecological fitting than under co-introduction scenarios.

Rates and severity of impacts may be further enhanced under co-introduction scenarios, which are characterized by multiple, potentially strong, positive feedbacks between co-invading partners that are absent under ecological fitting scenarios (Fig. 2). Legumes that nodulate abundantly may cause a rapid build-up of their associated co-introduced rhizobia, amplified by indirect effects through changes in soil abiotic and biotic conditions as a result of, for example, leaf litter feedbacks and subsequent nutrient enrichment (e.g. Yelenik *et al.*, 2004). This effect might reduce potential lag times associated with establishment of interactions with resident rhizobia in novel soils, as well as feeding back positively into increased non-native legume performance. The presence of co-introduced alien rhizobia also opens up the possibility for

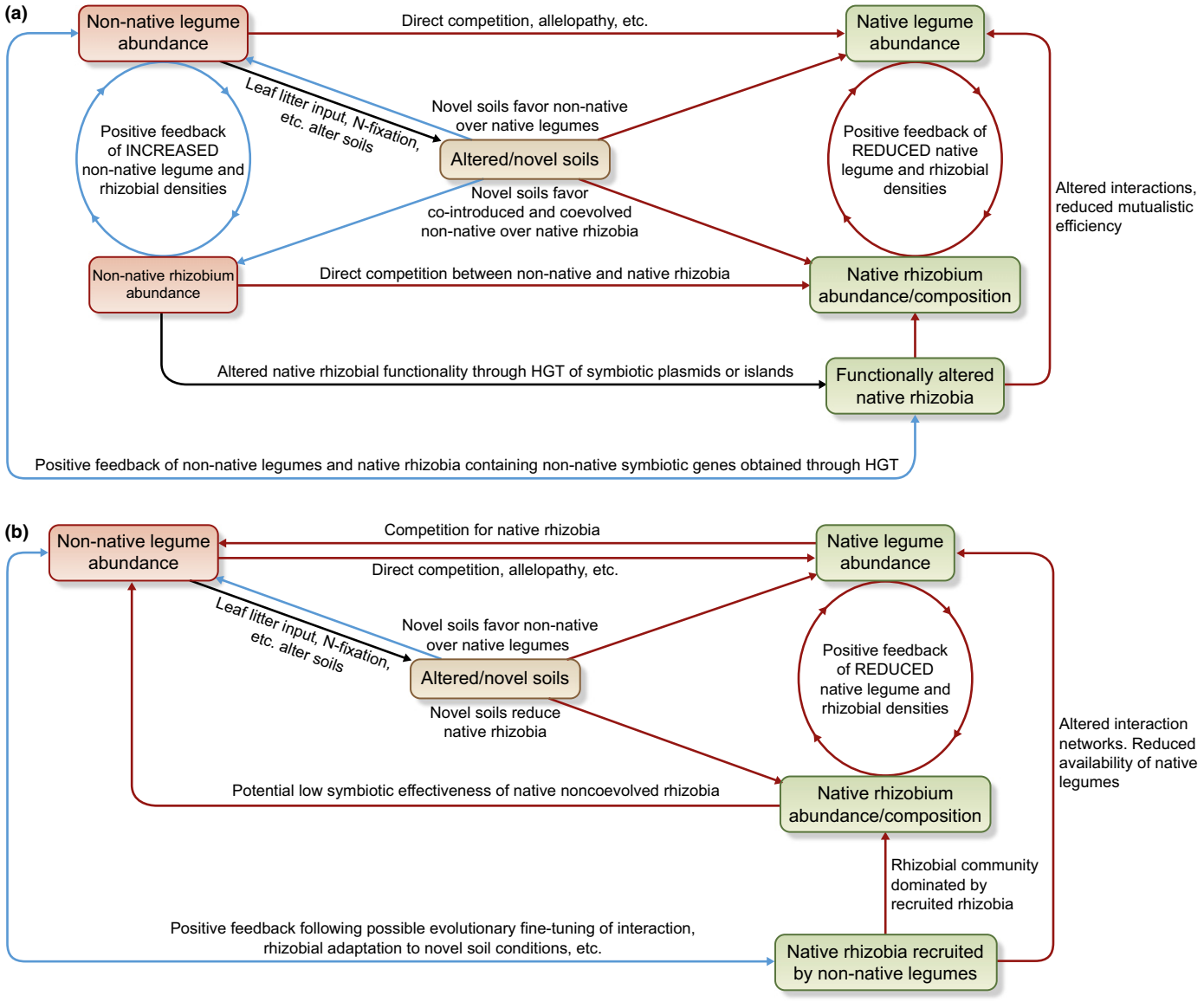


Fig. 2 Mechanisms of invasion impacts on native legumes and their associated rhizobia under two alternative pathways, (a) co-introduction (cf. Fig. 1a, Scenario A) and (b) ecological fitting (cf. Fig. 1a, Scenario C), for establishing mutualistic interactions during legume invasion. Blue arrows indicate direct positive influences and red arrows indicate direct negative effects. Black arrows indicate the processes through which non-native legumes alter soils and native rhizobial functionality during invasion, thus resulting in indirect impact pathways. Note the multiple strong positive feedback loops under co-introduction and additional impacts associated with the presence of invasive rhizobia (through direct microbe–microbe competition and functional changes to native microbes through horizontal transfer of symbiotic genes). HGT, horizontal gene transfer.

invasive legumes to recruit native bacteria (which are potentially better adapted to local abiotic conditions) following HGT of symbiotic gene islands from non-native to native bacteria (e.g. Horn *et al.*, 2014; Ling *et al.*, 2016). The effectiveness of N-fixation in native legumes may be further compromised if HGT leads to less effective symbiotic interactions (e.g. Rodriguez-Echeverria *et al.*, 2012), for example through altered chemo-attraction, amplified as invasive legumes become dominant in invaded communities. The net effects of these positive feedbacks between two invaders is to enhance invasion impacts common to both co-introduction and ecological fitting pathways, that is, direct and indirect plant–plant effects, indirect plant–microbe effects, and disruption of native legume–rhizobium interactions (Fig. 2). Finally, co-introduction introduces an additional impact avenue – the direct effects of non-native rhizobia on native rhizobia – which is absent under ecological fitting. Recent evidence suggests that direct competitive effects and competition for nodulation opportunities may be profound (Barrett *et al.*, 2015). Such perceived competitive exclusion of native rhizobia by non-native ones (or changes in abiotic conditions favoring co-introduced rhizobia) could explain the results of a recent observational study in South Africa which showed dramatic compositional changes of native legume nodule communities under *Acacia* invasions (fast-growing alpha bacteria were present in *c.* 50% of nodules in pristine sites but absent from adjacent invaded communities) (Le Roux *et al.*, 2016). Interestingly, this study also found that specialized native legumes did not persist in invaded sites, while generalists could persist, but in association with compositionally different rhizobia. Under the co-introduction scenario, reduced diversity of rhizobial associates, compared with the host plant's native range, might also promote higher symbiotic effectiveness as host plants could avoid exploitation/nodule co-infection by less effective strains (Barrett *et al.*, 2015).

V. Concluding remarks and future directions

Whilst research on impact pathways is in its infancy, and evidence supporting our contention that impacts under co-introduction scenarios should be faster and more severe is currently limited, this idea is nonetheless intuitive. In contrast to ecological fitting, co-introduction scenarios involve multiple invaders interacting synergistically, establishing positive feedbacks that may promote further invasions (i.e. invasional meltdown), for example secondary colonization by nitrophylic grasses (Yelenik *et al.*, 2004), and therefore open up multiple additional avenues to impact.

While the majority of evidence suggests that invasion of legumes is not often limited by their ability to establish effective rhizobium symbioses (Keet *et al.*, 2017, and references therein), the jury is still out on how often this involves co-introduction vs ecological fitting. Establishing which of these pathways are involved is important, because it may have strong consequences for both the pace of invasion and the extent and rate of subsequent impacts. Future research should thus focus on determining whether co-introduction of mutualist partners is frequent, and on ascertaining the existence of strong positive feedback effects and direct effects of non-native on native microbes under co-introduction. Recent advances in next-generation sequencing DNA barcoding of microbiomes provide a powerful tool to address some of these biogeographically linked research questions. This also opens the door for much-needed experimental research to determine the effects of rhizobial provenance (native vs non-native) on non-native legume performance. The inclusion of nonsymbiotic root nodule bacteria in such experiments may also provide exciting opportunities to test novel, but until now overlooked, aspects, such as the role of release from pathogens or cheaters in explaining non-native plant establishment success. Contrasting legume–rhizobium network structures based on bacterial identity alone (e.g. housekeeping genes) and those based on functionality (e.g. nodulation genes) also offer exciting opportunities to assess impacts of HGT on biotic interaction networks and particular mechanisms that allow network infiltration. The effects of co-introduction vs ecological fitting on the invasion dynamics of legumes also have important management consequences; the former should be prioritized for eradication efforts given the rapidity and extent to which impacts may manifest, and, where possible, such co-introductions should be avoided. Moreover, legumes that readily nodulate effectively with widely applied commercial crop inocula may pose a significantly larger risk of establishing successful symbiosis in the absence of mutualist co-introduction. Finally the principles we outline here are not limited to legume–rhizobium interactions, but can guide thinking about pathways of establishment of any kind of mutualisms in invasion scenarios and their consequences for the severity and pace of invasion impacts.

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